The Genomic and Cultural Diversity of the Inka Qhapaq Hucha Ceremony in Chile and Argentina

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Abstract

The South American archaeological record has ample evidence of the socio-cultural dynamism of human populations in the past. This has also been supported through the analysis of ancient genomes, by showing evidence of gene flow across the region. While the extent of these signals is yet to be tested, the growing number of ancient genomes allows for more fine-scaled hypotheses to be evaluated. In this study, we assessed the genetic diversity of individuals associated with the Inka ritual, Qhapaq hucha. As part of this ceremony, one or more individuals were buried with Inka and local-style offerings on mountain summits along the Andes, leaving a very distinctive record. Using paleogenomic tools, we analyzed three individuals: two newly generated genomes from El Plomo Mountain (Chile) and El Toro Mountain (Argentina), and a previously published genome from Argentina (Aconcagua Mountain). Our results reveal a complex demographic scenario with each of the individuals showing different genetic affinities. Furthermore, while two individuals showed genetic similarities with present-day and ancient populations from the southern region of the Inka empire, the third individual may have undertaken long-distance movement. The genetic diversity we observed between individuals from similar cultural contexts supports the highly diverse strategies Inka implemented while incorporating new territories. More broadly, this research contributes to our growing understanding of the population dynamics in the Andes by discussing the implications and temporality of population movements in the region.

Key words: paleogenomics, Andes, Inka, population genomics.

Significance

While the expansion of the Inka empire across South America (14th century CE) transformed the socio-cultural and demographic landscape of the region, there is limited understanding of how human genetic variation was impacted. Our paleogenomics research on individuals associated with the Inka ceremony known as *Qhapaq hucha* reveals high heterogeneity in their genetic affinities, reflecting a complex scenario of interactions both before the Inka period, and later between the Inka and local populations. More broadly, this research contributes to our growing understanding of the population dynamics in the Andes by discussing the implications and temporality of population movements in the region.

Introduction

The South American archaeological record has ample evidence of the profound socio-cultural and demographic dynamism of past human populations in the region. This dynamism intensified in later periods, particularly with the establishment of agricultural and ceramic technologies (Scaffidi and Knudson 2020). From a genetic perspective, mitochondrial DNA (mtDNA) and genome-wide data have suggested different degrees of population continuity (de la Fuente et al. 2018; Moreno-Mayar et al. 2018; Posth et al. 2018; Nakatsuka, Lazaridis, et al. 2020; Nakatsuka, Luisi, et al. 2020) as well as evidence of gene flow and population interactions at both broad and regional scales. Examples of broad-scaled interactions include: (i) genetic affinity between ancient individuals from the Channel Islands in California and the Central Andes by 4200 BP (Posth et al. 2018); (ii) evidence of additional Mesoamerican-related ancestry in several South American populations (Moreno-Mayar et al. 2018); and (iii) a north-to-south gradient of ancestry associated with populations from central Chile in South Patagonian populations (Nakatsuka, Luisi, et al. 2020). Meanwhile, most of the interactions at a regional scale have been associated with empire states such as Tiwanaku and Inka. In the case of Tiwanaku, this has been reflected as an excess of allele sharing between ancient individuals from Tiwanaku administrative center and the highland region of South Peru compared to other regions (Nakatsuka, Lazaridis, et al. 2020). In addition, ancient genomes from Cusco analyzed by Nakatsuka, Lazaridis et al. (2020) and dated to the Inka period, showed genetic heterogeneity, reflecting the cosmopolitan nature of the empire's capital. Similarly, a recent paleogenomics study of the Machu Picchu site showed that individuals buried there "exhibited ancestries from throughout the Inca Empire" (Salazar et al. 2023).

Of all the cultural developments in South America, the Inka stands out as one of the most monumental and largest empires in the region. Expanding from its capital Cusco around the 14th century CE, the Inka empire, or *Tawantinsuyu*, rapidly spread north, reaching present-day southern Colombia, and south, reaching the central-south region of present-day Chile and central-west Argentina (Pärssinen 2018; Raffino et al. 2020). Evidence of its advance is well documented through different elements, especially styles, and iconography on different materials such as ceramics and textiles. In addition, the *Qhapaq ñam*, or the Inka trail, is an extensive network of roadways that bears witness to the high connectivity and expanded influence of the Inka throughout the Andes (Covey 2008).

The *Tawantinsuyu* encompassed a territory of nearly 1,000,000 km² and was divided into four major regions: *Chinchaysuyu* (north), *Antisuyu* (east), *Collasuyu* (south), and *Cuntisuyu* (west), exhibiting significant variability in regional human populations, landscapes, and climates. This diversity not only provided the Tawantinsuyu access to a wide range of resources but also necessitated interactions with diverse populations with distinct political, social, cultural, and economic practices. As a result, the Inka devised varying annexation strategies for each region (Williams and Castellanos 2020), as evidenced in the archaeological record, including direct or "territorial" strategies and symbolic or hegemonic ones. The first category includes, for example, infrastructure in previously occupied and unoccupied areas, such as administrative buildings, relocation of people and resources, and productive activities. Meanwhile, symbolic strategies have been described through the Inka appropriation of local spaces either by diplomacy -by promoting specific ethnic leaders or groups-, resignification and symbolic claiming of sacred spaces, or conflict (Williams and D'Altroy 1998; Hayashida 2003; Alconini 2013; Pavlovic et al. 2019; Williams and Castellanos 2020). The dynamics of interaction and domination fluctuated, based on both the *Tawantinsuyu*'s interests and the unique characteristics and motivations of the local populations (Hayashida 2003; Pavlovic et al. 2019; Williams and Castellanos 2020). Moreover, there is evidence of simultaneous implementation of different coordinated policies to assert dominance over a single territory (Hayashida 2003; Covey 2008; Williams and Castellanos 2020).

During the Inka expansion, some of the highest mountains in the Andes became places of special meaning, reaching their highest expression through a ritual known as *Qhapaq hucha*. As part of this ritual, one or more individuals, usually younger than 16 years old, were buried close to the summit, together with an assortment of grave goods of local and foreign origin. It has been proposed that these sacrifices marked the culmination of a ceremonial pilgrimage that originated in the heart of the *Tawantinsuyu* capital, Cusco (Castro and Ceruti 2018). Across the empire's range, there are at least 14 summits with human burials and the region of *Collasuyu* stands out for its high incidence. Accompanying these human offerings are secondary tributes such as camelid or anthropomorphic figurines crafted from *Spondylus* shells, minerals such as silver or gold alloys, food items, coca leaves, feathers, textiles, and pottery (Mostny 1959; Reinhard and Ceruti 2005; Ceruti 2007; Beorchia Nigris and Vitry 2016; Castro and Ceruti 2018).

The presence of high-altitude shrines has often been interpreted as being indicative of Inka influence and dominion. Through rituals conducted at the base and summit of mountains, the Inka not only appropriated these spaces but also reshaped the ritual landscape, forging stronger connections with local populations (Acuto 1999; Ceruti 2007; Ibacache et al. 2016). Interpretations of the implementation and motives for conducting *Qhapaq hucha* across the Inka territory vary widely. These rituals have been seen as demonstrations of dominion over newly acquired lands, as acts of foundational importance, and as preventative measures against disasters like earthquakes, volcanic eruptions, and droughts. Additionally, they have been associated with specific events such as fertility ceremonies for livestock and crops (Castro and Ceruti 2018). The presence of these rituals has also been correlated with areas rich in mineral resources (Cruz et al. 2013) or with regions where Inka influence had recently been established, resulting in limited administrative centers and structures dedicated to solar ritual ceremonies (Covey 2018). Importantly, little is known about the individuals buried as part of this ceremony, including their origins.

This work aims to investigate the practice and diversity of the *Qhapaq hucha* ceremony through a genetic lens, by characterizing the genetic variation and regional affinities of the individuals associated with these burials. In particular, by implementing a paleogenomic approach, we evaluate the genetic relationships of the individuals associated with the *Qhapaq hucha* ceremony with each other, as well as with other past and present-day populations across South America. More broadly, this research contributes to the understanding of the ancient population dynamics in the Andes by discussing the implications and temporality of population movements in the region.

Results

Whole-genome sequencing data from three individuals who have been culturally associated with the *Qhapaq hucha* (QH) ceremony in Chile and Argentina were analysed, of which two were newly sequenced in this study and one was published previously (Table 1 and supplementary tables S1 to S2, fig. S1, Supplementary Material online). We observed that the endogenous content of these newly sequenced individuals is quite high, reaching values above ~60%. While these values are quite exceptional for ancient DNA, it is important to consider these individuals were buried at high altitudes and were frozen for several centuries. Furthermore, they are all about 500 years old, and once in the museums, they have been kept under controlled environmental conditions to avoid further degradation. They displayed the characteristic damage patterns (supplementary fig. S1, Supplementary Material online), and contamination estimates through the mitochondrial DNA are below 5% (supplementary table S2, Supplementary Material online).

Table 1 Summary of the Qhapaq hucha-associated individuals analyzed in this study

Summit	DoC*	Genetic sex	mtDNA haplogroup	Y-chromosome haplogroup
Cerro El Toro	3.6×	XY	D1j1a1	Q1a2a1a1
Aconcagua**	2.4×	XY	C1bi	Q1a2a1a1
Cerro El Plomo	2.2×	XY	C1b	Q1a2a1a1

See extended sequencing and mapping statistics in supplementary table S2, Supplementary Material online. *Depth of coverage; **Moreno-Mayar et al. (2018).

First, the uniparental signatures of these individuals were analyzed and compared to present-day distributions of the assigned haplogroups in South America. All mitochondrial lineages belonged to known haplogroups in South America (C1b and D1j), some of which show a more restrictive distribution. The lineage C1b*i* in the Aconcagua individual was first characterized by Gómez-Carballa et al. (2015). This specific lineage was not found in any present-day population, which the authors interpreted as the result of insufficient sampling or demographic events since the Inka. However, the lineage C1b is one of the most frequent lineages in South America (Gómez-Carballa et al. 2015). The lineage of the El Plomo individual is also part of C1b but it presents unique variations not overlapping with the ones described for the Aconcagua child. Meanwhile, the lineage D1j1a1 characterized in the El Toro individual shows higher frequencies in northwestern and central Argentina (Bodner et al. 2012; García et al. 2012; Nores et al. 2022). The Y-chromosome haplogroups were characterized for the three individuals, all belonging to the main lineage in the Americas Q1a2a1a1.

The genomes of the three QH individuals were analyzed together with 652 individuals from different present-day populations (supplementary table S3, Supplementary Material online). A principal component analysis (PCA) was performed using *smartpca* in Eigensoft (Patterson et al. 2006), restricted to present-day populations from Peru, Chile and Argentina (Fig. 1a). The first two principal components (PCs) described two major genetic ancestry gradients in South America:

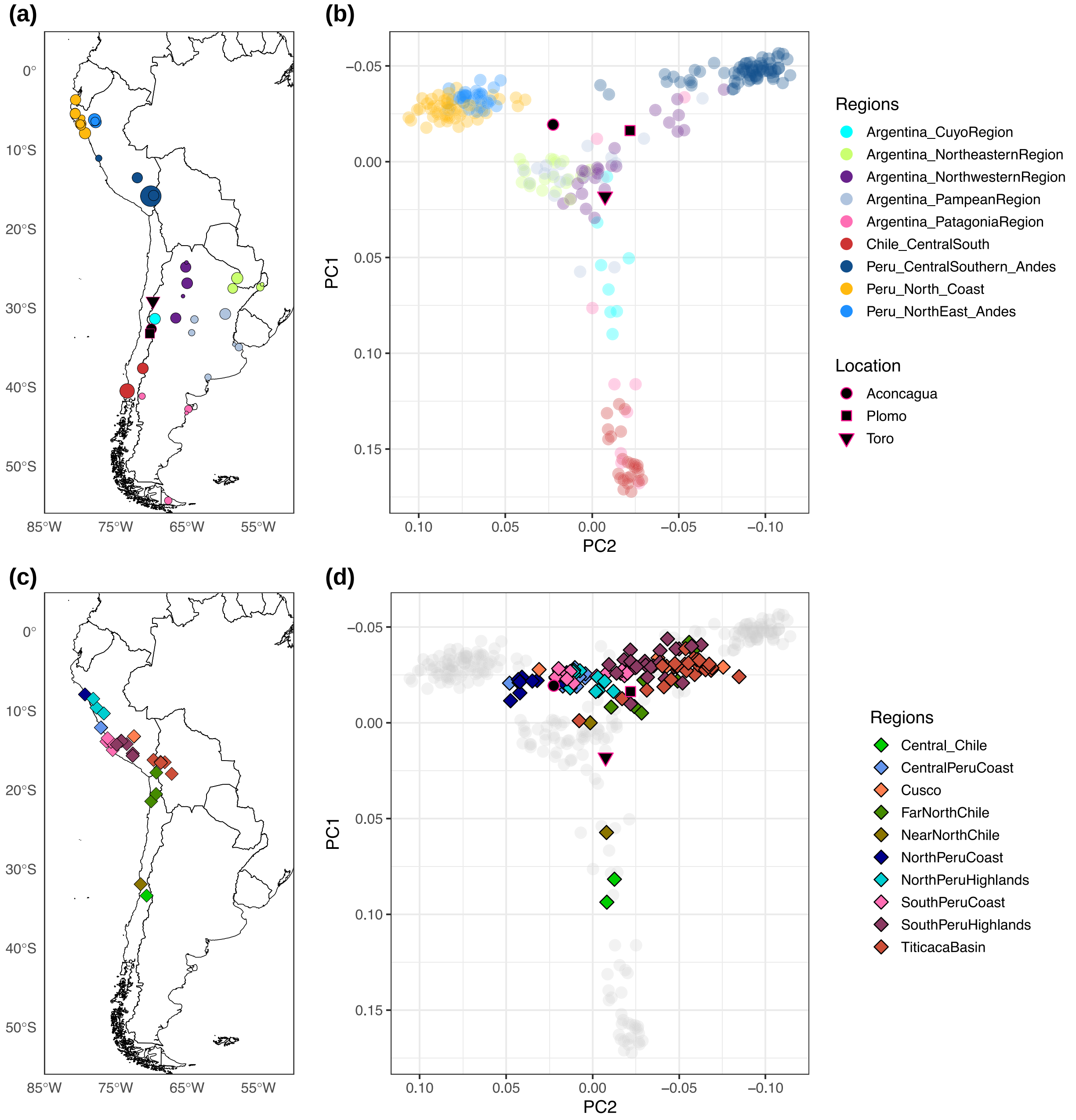

Fig. 1. Map and principal component analysis (PCA). a) Locations of the QH-associated burials analyzed in this study. Additionally shown are the geographic distribution of present-day populations included in the analysis, with the size of the circle is indicative of the sample size (the smallest circle is one individual); b) PCA of QH individuals, projected onto PCs 1 and 2 estimated with present-day populations that are color-coded by region; c) Geographic distribution of published ancient genomes included in the analyses; d) PCA of the published ancient genomes and the QH individuals projected onto PCs 1 and 2 estimated with present-day populations.

PC1 showing a north-to-south distribution with individuals from Peru at one end and individuals from central-south Chile at the other; and PC2, separating individuals from northern and southern Peru (Fig. 1b). The three ancient QH genomes and nearly 200 ancient individuals from Peru, Bolivia, and Chile (see details in supplementary table S4, Supplementary Material online) were projected onto the PC space described in Fig. 1b using the lsqproject option in *smartpca* (Fig. 1c). The QH individuals fall at different positions along the genetic gradients, suggesting they have different genetic affinities within South America (Figs. 1b and d). Other ancient genomes from South America generally cluster based on their geographical locations, as described elsewhere (Nakatsuka, Lazaridis, et al. 2020).

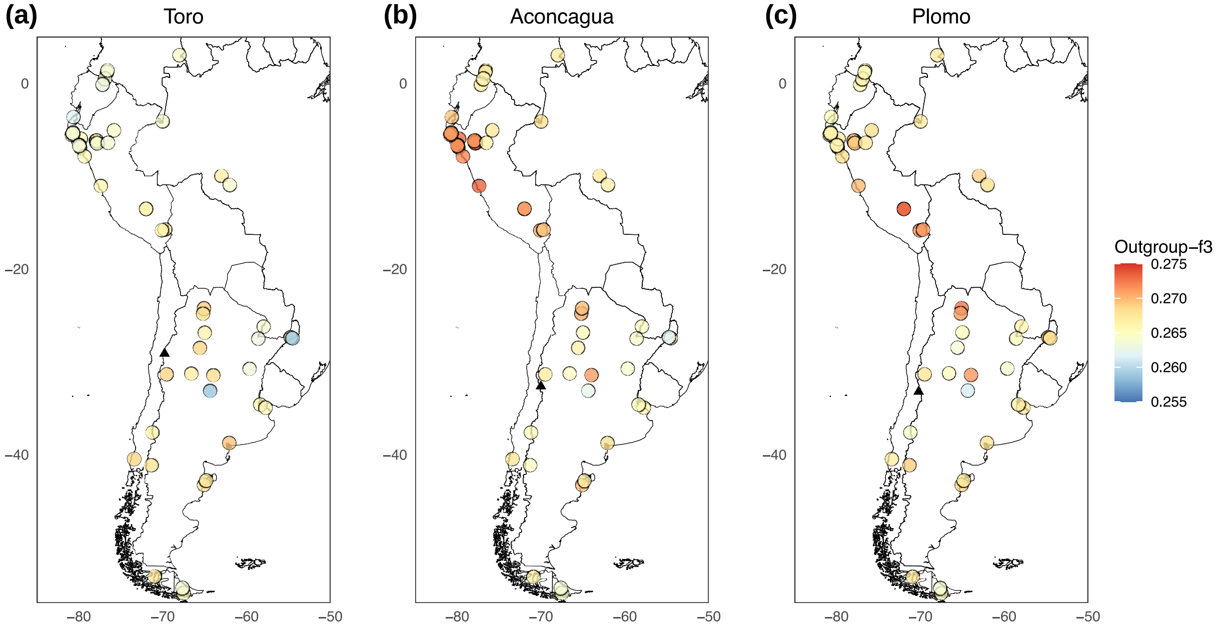

Fig. 2. Outgroup-ƒ3 analysis. The analysis was performed with the software admixtools (Patterson et al. 2012) of the form ƒ3(QH, X; Outgroup), where QH represents each of the three ancient genomes associated with the *Qhapaq hucha* ceremony and X represents different present-day populations from South America. The black triangle shows the geographical location of each QH individual.

We evaluated the genetic affinities of the QH genomes to populations from South America using an outgroup-ƒ3 statistic of the form (QH, X; Outgroup), with X representing diverse present-day and ancient individuals from South America, and Yoruba used as Outgroup. Figure 2 shows the results of this analysis for only present-day populations as X (see also supplementary fig. S2, Supplementary Material online). El Plomo individual shows a stronger association with populations from central-south Peru, while El Toro individual displayed the highest outgroup-ƒ3 values with present-day populations from northwestern and Cuyo region in Argentina and southern latitudes, and Aconcagua shared the greatest genetic affinities with present-day northern and central Coast populations from Peru. The latter has been reported in other studies (Moreno-Mayar et al. 2018; Nakatsuka, Lazaridis, et al. 2020).

In addition, we generated a multi-dimensional scaling (MDS) plot of a distance matrix, based on the outgroup-ƒ3 statistic converted to distance (1—outgroup ƒ3), between pairs of ancient individuals from South America, keeping only individuals with at least 10% of the data, which correspond to 160,000 positions (supplementary fig. S3, Supplementary Material online). As shown previously (Nakatsuka, Lazaridis, et al. 2020), we observed that the clustering of ancient individuals mostly followed a pattern based on major geographical regions (e.g. Titicaca basin, south Peru highlands, North Peru highlands). We observed QH individuals clustering with different ancient groups, reflective of the analysis with present-day populations. Overall, the outgroup-ƒ3 analysis suggests that each QH individual shares genetic similarities with different present-day and ancient groups across South America (supplementary fig. S2 to S4, Supplementary Material online).

To evaluate in detail the different genetic affinities between QH individuals, we implemented a *D*-statistic analysis of the form *D*(QH1, QH2, X; Outgroup), where QH1 and QH2 represent pairs of QH individuals, X is a subset of present-day individuals from South America, representing the different regions and genetic clusters on the PCA, and Yoruba was used as Outgroup (Fig. 3, supplementary fig. S5, Supplementary Material online). Compared to the other QH individuals, the Aconcagua individual is closer to present-day individuals from the north coast of Peru (e.g. Eten). The El Plomo individual mostly shows significant ($|Z| > 3$) allele sharing with present-day individuals from central-south Peru when compared to the El Toro individual. Meanwhile, there is no tested present-day population closer to El Toro than any of the other QH individuals.

Similarly, we evaluated the genetic affinities of QH individuals with each other and with other ancient individuals available in the literature using the *D*-statistic, observing a similar pattern. However, most of the results were not statistically significant, with absolute Z-scores lower than 3 (see supplementary fig. S6, Supplementary Material online). In contrast to the tests with present-day individuals, we observed two ancient groups that were consistently closer to the El Toro individual: LosRieles_5100BP and Conchalí_700BP. In addition, we re-analyzed shotgun sequencing data generated for three ancient individuals from the same province in

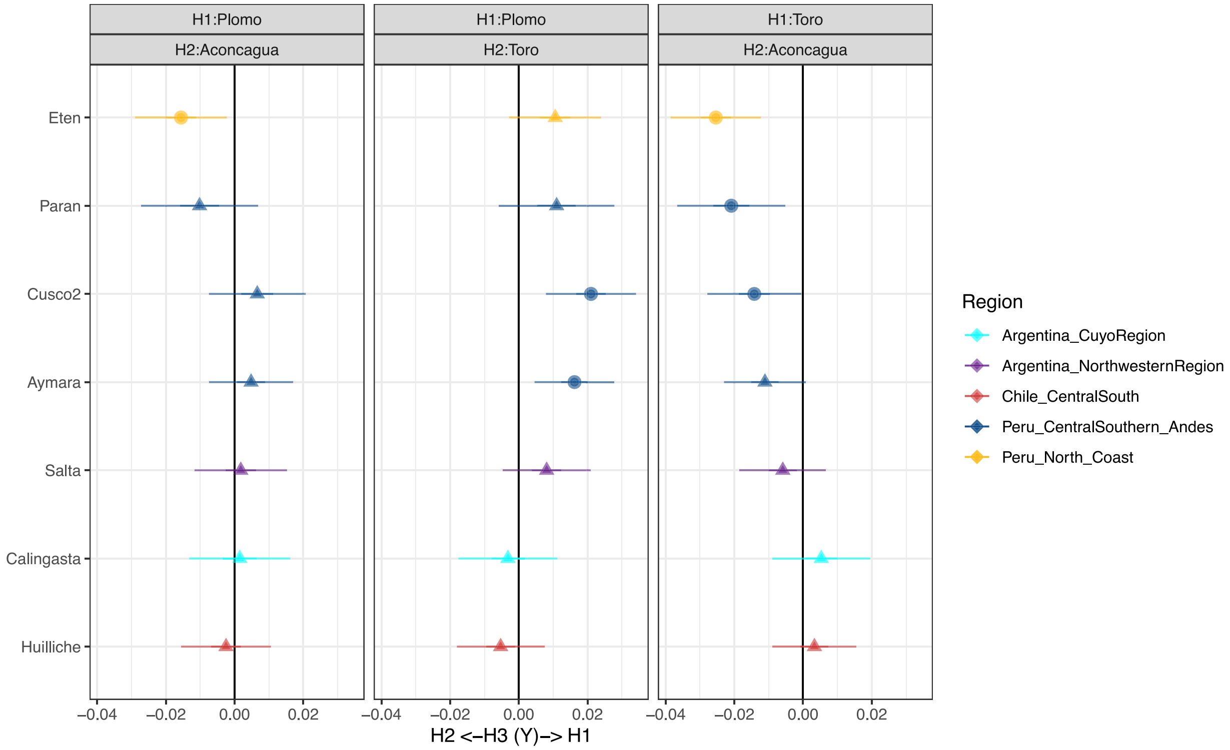

Fig. 3. *D*-statistic of the form *D*(Qh1, Qh2; X; Outgroup). QH1 and QH2 represent pairs of *Qhapaq hucha* individuals and X represents different present-day populations from South America. The error bars represent 3 SEs. In circles, we display values with an absolute z-score higher than 3, while in triangles, we show those lower than 3. The analysis was performed using the software admixtools (Patterson et al. 2012). Extended version in supplementary fig. S4, Supplementary Material online.

Argentina (San Juan) and dated to *ca.* 1500 to 2000 cal BP (Pedersen et al. 2022). Despite the low depth of coverage (0.006× to 0.3×) and quality of these genomes, we found their genetic affinities to be similar to the ones observed in the El Toro individual (supplementary fig. S7, Supplementary Material online and S8). Furthermore, while the absolute Z-scores are not statistically significant, they displayed a trend toward the El Toro individual (supplementary fig. S6, Supplementary Material online).

Using qpWave, we assessed whether QH individuals form a clade with respect to a set of populations referred to as "Right populations" (Harney et al. 2021) (supplementary table S5, Supplementary Material online). Using a broad geographical and temporal set of right populations (Set1) similar to the model implemented by Posth et al. (2018), all QH individuals form a clade with each other (Figure S9A, *P*-value > 0.05). However, when selecting a more informative list of populations to provide greater regional resolution (Set2), we observed that none of the QH individuals form a clade with each other (Figure S9B, *P*-value < 0.05), supporting the ancestry differences between these individuals reported in our previous analyses. We next used a subset of Set2 with more regionally relevant groups and, again, found that this set was able to distinguish between two pairs of QH individuals, to the exclusion of the El Plomo and El Toro individuals (Set 3.1, supplementary fig. S9c, Supplementary Material online). Since LosRieles_5100BP or Conchalí_700BP were the two ancient genomes that were significantly closer to El Toro compared to the other QH individuals in the *D*-statistics analysis (supplementary fig. S6, Supplementary Material online), we reintroduced these two genomes consecutively into Set3.1 to test if we were able to achieve better resolution of the genetic lineage contributing to El Toro (Sets 3.2 and 3.3). As expected, we observed that we were only able to differentiate between the El Toro and El Plomo individuals when either the LosRieles_5100BP or Conchalí_700BP genomes were included in the set (supplementary fig. S9c–e, Supplementary Material online). This may suggest that the genomes of these two individuals (Los Rieles dated 5100 BP and Conchalí dated 700 BP) represent a distinctive lineage contributing to QH-related individuals.

We further explored the relationship between QH individuals and other present-day individuals from South America using qpGraph. We started by exploring different models for a set of present-day individuals and each QH individual in the R package ADMIXTOOLS2 (Maier et al. 2023). Then, the parameters of the model (branch lengths and admixture proportions) were optimized using qpGraph in the software ADMIXTOOLS (Patterson et al. 2012). We evaluated different topologies based on the worst Z-score and the presence of

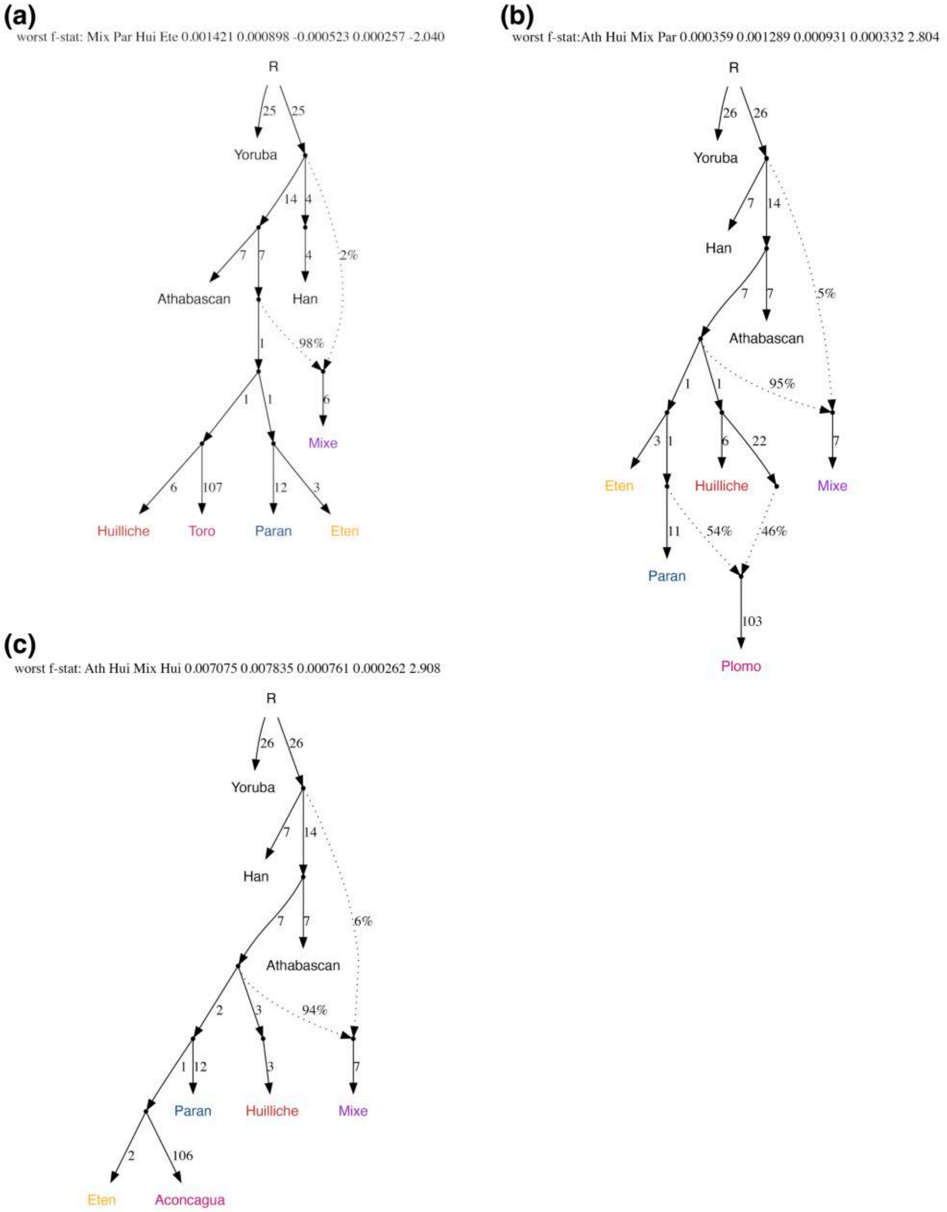

Fig. 4. Admixture graphs. a) Best-fit graph for El Toro individual (maximum |Z-score| = 2.04); b) Best-fit graph for El Plomo individual (maximum |Z-score| = 2.8); c) Best-fit graph for Aconcagua individual (maximum |Z-score| = 2.9). Additional models are shown in supplementary fig. S9 to 13, Supplementary Material online.

zero-length internal branches, as well as incorporating information from our analyses about the relationship between these populations. For example, we were able to replicate the gene flow from an unsampled population (UPopA) into Mixe (Moreno-Mayar et al. 2018; Villa-Islas et al. 2023). Within South America, we included representatives of the north coast of Peru (Eten), central-south Peru (Paran), and central-south Chile (Mapuche-Huilliche). Figure 4a-c summarizes the best-fit models for each QH individual. Consistent with our previous results (Figs. 1 to 3), the different genetic affinities of each QH individual are clearly observed in the presented models. We could not find a good fit for the El Toro individual with a present-day population from Northwestern or the Cuyo region in Argentina due to the high amount of missing data after masking the present-day data for European admixture (see Methods for details on masking). However, following up on the outgroup-$f3$ results, we included Mapuche-Huilliche from the central-south region in Chile as one of the present-day populations with the highest genetic affinity to the El Toro individual and observed that this individual is cladal to a lineage represented by present-day Mapuche-Huilliche (Fig. 4a and supplementary fig. S10, Supplementary Material online). Since El Plomo individual showed a high genetic affinity with central-south Peru populations, we first evaluated an unadmixed model, mostly obtaining absolute Z-score values higher than 3 (supplementary fig. S11, Supplementary Material online). The model that finally produced the best fit for El Plomo involves an admixture event between a lineage close to Paran and another one close to Mapuche-Huilliche (Fig. 4b and supplementary fig. S12, Supplementary Material online). Complementary, we evaluated the best-fit qpGraph models of El Plomo or El Toro (Fig. 4a and b, respectively) with other ancient individuals as targets. In particular, we used the genomes from Conchalí_700BP and Pukara-6_700BP (Nakatsuka, Lazaridis, et al. 2020) as the groups that are geographically closer or share the highest genetic drift to the El Plomo, respectively. For Conchalí_700BP we used the best-fit graphs of El Plomo and El Toro. Both models provided a good fit (supplementary fig. S13a–d, Supplementary Material online), but in the best-fit model of El Plomo the admixture percentage from the Paran-related lineage into the Conchali group was very low in contrast to ~57% into El Plomo (0% with the full data and 3% with transversions only). We next ran a *D*-statistic of the form D(Huilliche, Conchalí; X, Yoruba) where X represents different present-day populations from central-south and coastal Peru. There were no values significantly different from zero, suggesting no additional contributions from X into Conchalí (supplementary table S6, Supplementary Material online). The ancient individuals that have the highest shared genetic drift with the El Plomo child are located further north, in north Chile, particularly those from the site Pukara-6. However, the best-fit qpGraph model of El Plomo failed for these individuals, finding instead a better fit with the unadmixed model (supplementary fig. S13e–h, Supplementary Material online). Finally, a model of the Aconcagua individual suggested shared genetic ancestry with Eten, a present-day population representative of the north coast of Peru (Fig. 4c and supplementary fig. S14, Supplementary Material online).

We estimated the time of the admixture between the lineages represented by Paran and Mapuche-Huilliche in El Plomo using DATES (Chintalapati et al. 2022). We tested alternate models with modern sources representing central-south Peru to include other present-day populations than Paran that also shared high genetic drift with the El Plomo individual (Cusco, Cusco2, and Aymara). Additionally, due to potential biases introduced by recent demographic events in present-day populations, we replicated the admixture dating with ancient sources sharing the highest genetic drift with the modern sources (Paran and Mapuche-Huilliche), identified through an outgroup-$f3$ analysis (supplementary table S7, Supplementary Material online). For Mapuche-Huilliche, we selected two alternate ancient groups, Chile_Conchalí_700BP and Chile_LosRieles_5100BP, while we substituted Paran with South_Peru_Highlands and North_Peru_Highlands (Nakatsuka, Lazaridis, et al. 2020). Three pairs of sources provided a good fit by adhering to the following criteria (a) Z-score > 2, (b) $\lambda < 200$ generations, and (c) NRMSD < 0.7 (Chintalapati et al. 2022): Huilliche-Cusco, Huilliche-Aymara, and Chile_LosRieles_5100BP-South_Peru_Highlands (supplementary table S8, Supplementary Material online). The latter two pairs yielded a similar admixture time estimate of ~2000 to 2600 yr BCE, which suggests an admixture event between representatives of the central-south Peru and the central-south Chile lineages that predates the Inka period. On the other hand, while the Huilliche-Cusco pair yielded a younger estimate of ~72 yr CE, we speculate that this result may be impacted by recent drift or bottleneck in the present-day Cusco population as reported by Barbieri et al. (2019).

Finally, we evaluated parental relatedness and effective population size in the QH individuals compared to other ancient individuals in Chile, Peru, and Argentina using the software hapROH (Ringbauer et al. 2021). We observed that the QH individuals have very few runs of homozygosity compared to other individuals, suggesting rare close kin unions and large effective population sizes (supplementary fig. S15, Supplementary Material online).

Discussion

The *Qhapaq hucha* ceremony has been described as a religious and political mechanism of social control over the people that the Inka conquered as they expanded into new territories. The location of these ceremonial burials at high altitudes has been linked to a sense of adoration of the Andean peaks. While this was likely a widespread sentiment across Andean societies, the Inka were probably the first to systematically explore and use the Andean peaks to their advantage as can be testified by the number of roads and structures (e.g. tambos or platforms) that were built along the Andes (Castro and Ceruti 2018). The individuals associated with this ceremony were mainly children or young women, buried with a rich and diverse assortment of grave goods. Textiles of different kinds, anthropomorphic and zoomorphic figurines made of different metals or *Spondylus*, feathers of different birds, and pottery are some of the most common elements found in these burials (Castro and Ceruti 2018; Vitry 2020). It is particularly interesting that the material evidence from the burial contexts was very diverse, bringing together valuable elements from the different regions of the empire or territories that were in contact with the Inka and local populations.

The diversity of the offerings and the notability of the QH ceremony itself have triggered several discussions about the origin of the buried individuals, how they were chosen, and how was their journey to their final resting place. One hypothesis is that the individuals chosen for the ceremony migrated either from the capital or from other distant areas of the empire. Alternatively, these individuals could have been part of local communities, originating from regions close to the burial sites (Castro and Ceruti 2018; Socha et al. 2021). It is noteworthy that the origins of these individuals, whether socio-cultural, geographical, or biological, should be considered in light of the dynamic nature of not only the Inka period but also events and population interactions across the Andes that predated the Inka period. Our genomic analyses do not favor either of the aforementioned hypotheses, reflecting a more complex scenario of human movements and interactions in the ancient Andes. This is in agreement with the varied strategies the Inka implemented across the empire to incorporate new territories and integrate new people, including the resettlement of populations and the use of intermediaries to extend its influence. The resettlement of populations was an important strategy implemented by the Inka to consolidate their position, control new regions, and organize *mitmaqkuna* (displaced non-local individuals) laborers in relocated working camps (D'Altroy 2018). While this was an extensive practice and it is estimated that almost a quarter or a third of the population was resettled (D'Altroy 2018; Davidson et al. 2021), the number of people relocated, mode, and reason varied from region to region. Moreover, the clothing and grave goods accompanying these QH individuals are as diverse as their genetic affinities and several characteristics of the burials have contributed to evaluating their cultural affiliations and, by extension, the putative origins of the associated individuals.

The El Toro Summit is located in San Juan Province, in northwestern Argentina. Inka influence in the region has been dated to ca. 1475 cal AD, although proof of Inka presence here is sparse compared to other areas. In fact, it has been suggested that the Inka impact in this region was associated with imperial developments on the west side of the Andes (present-day Chile) (García et al. 2021). The individual buried at the summit was estimated to be 20 to 22 yr old at the time of death. This individual is not only older than other *Qhapaq hucha* individuals, but the funerary context is, in general, less diverse, consisting of only a few textiles and no figurines or pottery (Schobinger 1964). While the location of the burial at high altitude (6,120 masl) constitutes one of the main features of the ceremony, the individual's grave features and age have prompted suggestions that the El Toro individual may not have been related to the *Qhapaq hucha* ceremony or, at least, was not one of the main burials associated with the ceremony (Schobinger 2008). While there are only a handful of high peaks with human burials along the Andes ($N = 14$), they are all surrounded by several other structures of ceremonial or administrative nature, which could alternatively explain the presence of the El Toro burial (Ceruti 2007; Vitry 2020). Taken together, this implies that the El Toro individual may have either been involved in the *Qhapaq hucha* ceremony or may have served as *chaski* or messenger for the Inka, which is supported by osteological evidence of plantar keratosis that may have been caused by extensive walking, and possibly associated with a long journey or a high mobility during this individual's life (Schobinger 2008). The cultural elements found in association with the individual have been linked to either the *Cuntisuyu* (western range of the Inka Empire) or *Collasuyu* (southern range of the Inka Empire). Moreover, the manufacturing and material of the clothing and other elements of the funerary contexts show a resemblance to local groups (Schobinger 2008; Beorchia Nigris and Vitry 2016). In concordance with the archaeological evidence, the mitochondrial haplogroup (D1j) and genome-wide diversity of the El Toro individual suggest genetic affinities with present-day and ancient populations from northwestern and Cuyo region of Argentina and central/central-south Chile, regions that were part of the southern range of the Tawantinsuyu.

The child from Aconcagua, located in Mendoza Province, Argentina, was a 7 to 8-year-old boy found at 5,250 masl. Two radiocarbon dates have been published for this individual (see details in García et al. 2021), with different results and large confidence intervals. The R_Combine function from Oxcal 4.4.4 (Bronk Ramsey 2009), using the Southern Hemisphere curve (Hogg et al. 2020), provides an estimated age of 1426 to 1510 (76.3%), 1550 to 1559 (0.8%), and 1580 to 1623 (18.3%) cal CE. The body of this individual was wrapped in 18 pieces of textiles and accompanied by diverse grave goods, including textiles, and anthropomorphic or zoomorphic figurines made of metal and *Spondylus* (Quevedo and Duran 1992; Schobinger 1999). It has been argued that the textiles and footwear of the child linked him to the Peruvian central coast, particularly the Chancay culture, evidence used in support of a coastal origin for this individual (Schobinger 1999). In addition, isotopic analysis of hair from the individual suggested a terrestrial diet for the year and a half before their death and, based on less conclusive results from bone collagen, a mixed diet before that (Fernández et al. 1999). Overall, there is cultural evidence suggesting affinities with groups from the Peruvian coast, but the characterization of the individual's diet lacking a clear marine input is not concordant with this hypothesis. The genomic analyses suggest a genetic affinity of this individual with several present-day and ancient individuals from the Peruvian coast, which supports the cultural links described before and can be interpreted as evidence of long-distance movement of this individual from coastal Peru to their final burial location in Aconcagua in Argentina. These results are in agreement with a previous study (Nakatsuka, Lazaridis, et al. 2020). However, isotopic and morphometric evidence from the Uspallata Andean Valley (Mendoza Province in Argentina, near the Aconcagua mountain) support the arrival of migrants before the Inka expansion to the area, from about CE 1,280 until 1,420 (Barberena et al. 2020). While the origin of these migrants could not be identified, this result suggests a more complicated scenario of social interactions and human migrations that pre-dates the arrival of the Inka in this region. Additional paleogenetic data from the region is needed to evaluate if the long-distance movement possibly associated with the Aconcagua child is a consequence of an earlier, pre-Inka movement or if it is part of the resettlement strategy of the Inka.

The child from El Plomo, from Santiago in Chile, is the southernmost burial associated with the *Qhapaq hucha* ceremony. This child is an 8 to 9-year-old boy found at an elevation of 5,400 masl (Quevedo and Duran 1992) and dated to 1460 CE (Silva-Pinto et al. 2023). The grave goods accompanying the child are very diverse, including bags with feathers, coca leaves, hair, nails, and deciduous teeth, in addition to three zoomorphic and anthropomorphic figurines made of metal or *Spondylus*. The clothing and ornaments (silver bracelet and headdress) suggest an association with the *Collasuyu* (Quevedo and Duran 1992; Acevedo 2012). In addition, several multidisciplinary studies have been conducted to evaluate this individual's health and cause of death, suggesting good health and evidence of trauma associated with the child's death (Silva-Pinto et al. 2023). The genomic analyses conducted in this study suggest genetic affinities of the El Plomo child with present-day populations from central-south Andes and ancient individuals from northern Chile and south Peru highlands. Moreover, our results suggest that the El Plomo child may be part of a currently unsampled genetic lineage from South America. We modeled the lineage of the El Plomo child as deriving genetically from two distinct lineages, represented by present-day populations in central-south Peru and central-south Chile. Recent research suggests that present-day populations from central-south Chile are part of a lineage splitting from other South American lineages during the Holocene (Lindo et al. 2018; Arango-Isaza et al. 2023). In particular, the split between central-south Peru and central-south Chile lineages has been dated between 8200 and 9250 BP (7300 to 6250 BCE) (Lindo et al. 2018). This suggests that there was post-split admixture between these two lineages with the El Plomo child representing one such admixed lineage with the admixture date estimated to ∼2000 to 2600 yr BCE (4550 to 3950 BP). When evaluating the best-fit qpGraph model of the El Plomo child against a geographically closer ancient group (Conchalí_700BP) or an individual with the highest shared genetic drift (Pukara-6_700BP), we were not able to gain further resolution into this unsampled lineage.

During the Late Period (1400 to 1536 CE) in the area near El Plomo (Mapocho basin), archaeological evidence shows the expansion of socio-cultural networks and ideological interactions, suggesting a diversification of cultural groups or units, potentiated by the expansion of the *Tawantisuyu*. Circulation of objects on a large territorial scale, new ceramic shapes and iconographies, and the emergence of stone architecture are expressions of this phenomenon. It has been proposed that the Inka deployed ideological and political incorporation strategies toward local communities, primarily through distinctive ritual congregation activities tailored to the specific characteristics of each local group (Pavlovic et al. 2019). However, the material archaeological evidence by itself does not allow us to distinguish between displaced non-local individuals (*mitmaqkuna*) and representatives of the *Tawantinsuyu* in the Mapocho and nearby valleys who may have been both local or non-local in origin (Pavlovic et al. 2019). Additional genomic data from the area is needed to evaluate the impact of these interactions on the local genetic diversity, as well as to learn more about the lineage represented by the El Plomo child and its stronger genetic affinity with geographically distant groups.

While attempting to ascertain geographical origins using paleogenomics in South America, a few critical challenges emerge. Several sub-regions and time periods are poorly or not at all represented in the genetic record, limiting a more comprehensive comparative analysis with present-day and ancient populations. This limitation may lead to simplified models of genetic similarities and origins that are clearly challenged by the human population dynamism of the Inka period and the Andes region as well as known human movements in earlier periods. There is evidence of population movements and cultural interactions long before the Inka empire, since the Middle Horizon (ca. 500 to 2000 BCE) or even earlier (Knudson and Torres-Rouff 2014; Standen et al. 2018; Barberena et al. 2020; Scaffidi and Knudson 2020; Beresford-Jones et al. 2023). While previous research has suggested the establishment of genetic structure and genetic continuity more broadly in the Andes ca. 2000 yr ago (Nakatsuka, Lazaridis, et al. 2020), there is evidence of admixture and mobility throughout the region (e.g. [Salazar et al. 2023]). There are also indications of spatio-temporal genetic heterogeneity and movements in the genomes analyzed in this paper, some of which predate the Inka period. Moreover, while our analyses provide evidence of genetic affinities between the QH individuals and particular present-day or ancient individuals across the Andes, the presented genetic results are unable to shed light on the cultural identities or ethnicities of these individuals. Regardless of what the genetic results suggest, the final resting place of these individuals ultimately ties them to the particular territories where they were found. There was a clear intention to bury them there, with obvious implications for local communities and their histories and any speculations on these matters are beyond the realm of genetic investigations.

Finally, several concerns have been raised regarding the legal and ethical aspects of paleogenomics research in the Americas (e.g. [Bardill et al. 2018; Claw et al. 2018; Wagner et al. 2020; Ávila-Arcos et al. 2022; Kowal et al. 2023]). The destructive nature of these studies and fragmentary archaeological records stresses the importance of weighing the type and number of samples, clearly defining the particular research questions or hypotheses, and the well-planned application of current technologies. Similarly, there has been little to no record of the total number of samples taken and processed by various laboratories working on paleogenomic projects in this region versus what is eventually included in the final publications (e.g. samples that have failed to yield DNA). In this work, we aimed to evaluate the genetic diversity of individuals associated with the Inka ceremony known as *Qhapaq hucha*. In order to perform this research, we design the project by avoiding new destructive sampling. Instead, samples collected previously in 2005 by one of the co-authors (MM), with the aim of evaluating their genetic diversity using uniparental markers (mtDNA and Y-chromosome), were re-analyzed using next-generation sequencing technologies. Museums that previously authorized the research were re-contacted to inform about the new approach. Furthermore, we engaged in outreach activities to disseminate the results of this study and their implications prior to publication. In the process of disseminating the results of this research, we also learned more generally about some of the legal and ethical claims of Indigenous Peoples in Argentina concerning their Ancestors, and mostly associated with fights for their recognition and ancestral rights (Gnecco 2019; Curtoni 2022; Jofré 2022; Jofré and Gómez 2022). We stress the importance of dialogues with local researchers and Indigenous communities not only to seek approval for research but also to learn about the history of the region and to weigh the consequences of our research and narratives to present-day communities.

Overall, on a local scale, this study contributes novel results to our growing understanding of the nature of the *Qhapaq hucha* ceremony, with a focus on the genetic origins of the buried individuals. More broadly, it expands our knowledge of human genetic variation in South America prior to European colonization with the identification of a previously unsampled lineage as well as pondering the evidence or expectation of gene flow in the focal time period. Future archaeogenomics research implementing appropriate ethical and community-engaged strategies will provide greater resolution on the bio-cultural dynamics in the region.

Materials and Methods

Data Generation

No new samples were collected in this study. Whole genome data was generated from samples collected in 2005, initially studied using only mitochondrial DNA markers (D-loop). Museums were notified of the new study aims and methods and they agreed with implementing newer methodologies.

DNA extractions were performed from tissue (muscle) samples using the protocols described in (Moraga et al. 2010; Raghavan et al. 2015; Moraga et al. 2023). Double-stranded DNA libraries were built following the standard protocol from (Meyer and Kircher 2010) and sequenced on an Illumina MiSeq and NextSeq. All laboratory work and sequencing were performed at the Faculty of Medicine of Universidad de Chile. Pre-PCR work was carried out in a facility dedicated to the analysis of aDNA samples, which is isolated from laboratories working with DNA from present-day samples. This facility has positive air pressure (HEPA-filtered and UV-treated airflow) and UV lamps on all working surfaces. Samples and reagents were manipulated under a laminar flow cabinet and using disposable sterile plastics and consumables.

Raw sequencing reads were mapped to the human genome reference build hg19 and the mitochondrial reference rCRS using BWA (*aln* and seed disable). Unmapped reads and those reads with a mapping quality below 30 were removed using samtools. PCR duplicates were identified and removed using Picard MarkDuplicates. Finally, we used GATK for indel realignment and samtools calmd to generate MD tags. Misincorporation patterns and error rates were evaluated using mapDamage v2 (Jónsson et al. 2013) and ANGSD (Korneliussen et al. 2014), respectively. Contamination estimates were performed using the software contamMix (Fu et al. 2014). Pseudo-haploid calls were generated using ATLAS (Link et al. 2017) for all three ancient individuals (Aconcagua from BAM) and for all ancient genomes with available shotgun sequencing data (see supplementary table S4, Supplementary Material online). For those ancient genomes with only published SNP data (1240k panel), files were downloaded in eigenstrat format (see supplementary table S4, Supplementary Material online).

Reference Dataset

We compiled a database of 652 worldwide present-day individuals (supplementary table S3, Supplementary Material online) and 296 ancient individuals (supplementary table S4, Supplementary Material online) from South America. Since most present-day data was generated using different SNP arrays (Axiom LAT1 and Human Origin Affymetrix), this data was phased and imputed by array using TOPMed Michigan Imputation Server (Das et al. 2016). ADMIXTURE (Alexander et al. 2009) analysis was performed before and after imputation to evaluate any changes in their global ancestry (supplementary fig. S16, Supplementary Material online). We kept the sum of positions from both arrays and the 1240k positions from the aDNA enrichment panel, for a total of 1.6 M positions. Present-day South American individuals with more than 99% Native American ancestry (according to $K = 3$ in ADMIXTURE) were used as references together with individuals with more than 99% European or African genetic ancestry in order to estimate local ancestry using RFMix v2 (Maples et al. 2013) with the parameters described in (Luisi et al. 2020). Non-Native American genetic ancestry was masked and, unless otherwise indicated, all analyses were performed using this masked dataset.

Analyses

Principal Component Analysis was performed using smartpca from Eigensoft (Patterson et al. 2006), with ancient individuals projected using lsqproj = YES. All *f*-statistic-based analyses (outgroup-*f*3, *D*-statistic, qpWave, and qpGraph) were performed using the software ADMIXTOOLS (Patterson et al. 2012). For the qpGraph analysis, we started by exploring different models for a set of present-day individuals and each QH individual in the R package Admixtools2 (Maier et al. 2023). We started by computing *f*2 using the function extract_f2 and then exploring different seed graphs using the function find_graph. We set the following parameters: Yoruba was used as the outgroup and stop_gen was set to 100. The analyses were repeated using 1 and 2 admixture events. We favored models that were consistent with previous publications (e.g. Athabascan splitting earlier than the other populations in the Americas and the ghost adxmiture in Mixe). The seed graph was run using the following set of present-day populations: Yoruba and Han from 1000G dataset, Athabascan (Raghavan et al. 2015), Mixe (Mallick et al. 2016), Eten, Paran (Barbieri et al. 2019), and Mapuche-Huilliche (de la Fuente et al. 2018). The QH individuals were added to this seed graph in the most likely position considering the results of our other analyses. We tested different models iterating through different present-day and ancient individuals (supplementary figs. S10 to 14, Supplementary Material online) as representatives of the regions of interest (e.g. north coast Peru, central south Peru). The parameters of the final models (branch lengths and admixture proportions) were optimized using qpGraph in the software ADMIXTOOLS (Patterson et al. 2012). Plots were constructed using Graphviz (https://github.com/dreampuf/GraphvizOnline). The qpWave analysis was implemented in the R package Admixtools2 (Maier et al. 2023). Like qpGraph, we started by computing f2 using the extract_f2 function for each model separately. Then, we ran qpWave using the function qpwave_pairs, where the left parameter was the list of QH individuals (*N* = 3), and the right was a different list according to the models from supplementary table S5, Supplementary Material online. Results were plotted using Rstudio (http://www.rstudio.com/) and custom scripts. Finally, we performed a Run of Homozygosity (ROH) test using the software hapROH (Ringbauer et al. 2021) with the standard parameters described in https://pypi.org/project/hapROH/. For comparison purposes, we included ancient genomes from South America with at least 400,000 or more of the 1240K SNPs as recommended by the software developers.

Supplementary Material

Supplementary material is available at *Genome Biology and Evolution* online.

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Author Contributions

C.D.C., M.C., and M.M. designed the research; R.V. and M.M. provided funds and resources to perform the research; C.D.C., D.C., R.V., and M.M. performed the research and analyzed the data; C.D.C., C.C., M.R., M.C., and M.M. contributed to interpreting results; C.D.C., C.C., M.R., and M.M. wrote the paper with input from all co-authors. R.V.'s contribution was made while working at Universidad de Chile before moving to its current affiliation at Universidad de Talca.

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Conflict of Interest

The authors declare that they have no competing interests.

Data Availability

Data will be available for download through the European Nucleotide Archive (ENA) (accession no. PRJEB76127).

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